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SAP EXUDATION PHENOMENA OF THE ELM TREE

BY

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A THESIS SUBMITTED FOR THE DEGREE OF

MASTER OF ARTS

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I. INTRODUCTION

The phenomenon of excreting liquid water is widely distributed in the plant kingdom and may occur either from uninjured or from injured parts of plants as in the bleeding of cut stems. In the former case the water escapes as the result of the activity of glands, through stomata, or through other openings. Both bleeding and secretion of water is due to activities of living cells. There may be special groups of cells in the leaves or flowers which produce these secretions. This power of secretion is not confined to the higher plants. Various types of mosses, fungi, and even algae may also possess the power of exuding sap.

The process of exudation is probably not brought about in all cases in the same manner. The excretion of water, except in nectaries, is due not to the presence of dissolved substance outside the cell but to internal causes brought about by the activities of living protoplasm, the process being one of active excretion, active exudation, or filtration under pressure. According to Haberlandt (22), we have in the case of nectaries plasmolytic excretions due to the presence of sugar outside the cell. This type of excretion can be brought about and continued when the cell is flaccid while the other cases of excretion can only take place when cells are turgid. In both cases the osmotic powers of living cells are involved. Water may be forced

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into vessels, intercellular spaces, etc. from which it escapes in the liquid condition at the point of least resistance through pores, etc.

Haberlandt distinguishes between two kinds of hydathodes: the first being active hydathodes comprising epidermal water secreting organs such as unicellular and multicellular hairs or trichomes among Angiosperms and water glands of ferns. In these cases he thinks the energy employed in the process of secretion is supplied by the glandular hydathode cells themselves. Hence the exudation pressure in the water conducting system merely supplies the stimulus which sets the pumping action of the hydathode in operation. Lepeschin (36) believes this exudation is due to differences in permeability of cell membranes of the trichomes, that the sap of the outer cell by losing water becomes more concentrated and hence draws more water from next cell. Therefore the outer cells must have a more concentrated cell sap than the inner ones. In the case of epithelium hydathodes, Haberlandt says the process of secretion consists of a simple filtration, the energy being provided by root pressure or exudation pressure which may be set up in stems as well as roots. Here we see a similarity to Lepeschin's theory for the first, namely that the hydathode is merely a point of least resistance to filtration.

In the present paper only the phenomenon commonly termed bleeding will be considered and the term bleeding will be used

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to designate the exudation of liquid water under pressure from injured regions of plants such as may take place when stems, roots, or branches are injured from wounds by cutting, boring holes, mechanical injury, or other means.

II. REVIEW OF LITERATURE ON BLEEDING PHENOMENA

The phenomena of bleeding, because it is so easily observed, in maple, grape, vine, and birch, has been studied for several centuries. John Ray (46) was the first to observe the phenomenon while Hales (23) made a more extensive study of it. Ray and Hales observed bleeding in trees and vines only, while Hofmeister (25) showed that bleeding was possible from herbaceous plants as well. He also was the first to show that bleeding is possible in summer when transpiration is prevented. These investigators as well as Dutrochet (15) and Dassen (12) considered the active exudation of water to be due to the pressure caused by the absorptive activities of the roots and positive results were first obtained with root stocks and with single roots or even with root apices. Brücke (7) was the first to show that the bleeding in spring gradually decreased with the opening of the leaves, hence showing the relation of the turgid cells to leaf growth. He also found that there was considerable difference in pressure at different heights in a grape vine. For example, a manometer placed fifteen feet from the base of a vine

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would show less pressure than one placed five feet from the base.

Hofmeister (25) repeated Brücke's work and also experimented with various herbaceous plants. He showed that the same phenomena may be observed in any given plant even in small annuals which form little wood. By cutting off such plants as Ricinus, Tobacco, Digitalis, Nettle, Sunflower, Maize, and other cultivated plants when they are actively growing, and connecting a manometer to the cut end, he was able to get a marked pressure. He also noted that the stem soon stopped bleeding after the unfolding of its leaves, but that the roots may continue to bleed all summer. He describes the pressure as being due to endosmosis, brought about by organic substance such as gums, sugars, etc. which are stored in the medullary rays of the stem.

Baranetzky (2) checked up Hofmeister's work and devised some new methods of determining the periodicity of bleeding. He used two types of self registering apparatus to measure the sap exuded during the whole period of bleeding. The first type registered the amount by markings on a rotating cylinder. A small U tube was used to collect sap from a tube connected with cut stem. A float was suspended in the sap in the U tube to which a marker was attached which was kept in contact with the rotating cylinder. In this manner the amount of sap exuded at different periods of the day was

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registered. Another method devised by Baranetzky was the use of a revolving cylinder with two horizontal disks with holes at certain intervals into which small test tubes can be placed. This cylinder is connected to a clockwork which turns it at certain intervals just enough so the next test tube will be underneath the drainage tube which is connected with the stump of the decapitated stem. In this way the amount of sap exuded for each hour of the day can actually be measured.

By the above described methods Baranetzky was able to get the daily periodicity of bleeding. By keeping the temperature constant or by regulating the temperature he could test the effect of temperature fluctuation on the periodicity. His results show that with both constant and gradually changing temperature the exudation curve remains parallel to the temperature although the maximum and minimum were not always the same. However, with rapid changes the curves did not remain parallel. He concludes that the daily periodicity of sap exudation is not caused by the daily change in the soil temperature. That the small changes of this temperature can not change the curve of sap pressure since only by a change of 10°C will the normal process of bleeding be disturbed. Baranetzky thinks that there is a daily maximum and minimum for the plant and that each plant shows a maximum exudation at some definite time of the day. Young

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plants do not show such a definite period as older ones. This he concludes may be due to woody cells.

Baranetzky attributes the cause of bleeding to light instead of temperature fluctuations. In support of this theory he cites the results of three experiments he conducted with Helianthus tuberosus. First, he finds that etiolated branches of H. tuberosus bleed only slightly when subjected to normal light, temperature, and moisture conditions, and showed no periodicity. Second, he finds that if a plant be kept in the dark for ten days and then be exposed to light it shows the characteristic periodicity the first day but on succeeding days it does not exhibit any definite periodicity. Third, one of two normal plants of Helianthus was put in a dark room for nine days and then exposed to light in the forenoon only for twenty-five days. The other plant was exposed to light for thirty-five consecutive days during the afternoon periods only. The two plants were then put under the same conditions and the bleeding curves taken. The first plant reached its maximum flow earlier in the day and the second one reached it later in the day than normal control plants. Hence he concludes that exposure to light for different periods of the day has changed the time of day that the plant reaches its maximum flow.

Clark (9) was the first American to study the problem of bleeding to any extent. He, with numerous co-workers, made extended observations upon the amount, pressure, and

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composition of the sap which might be obtained from different species of woody exogens. He finds that the great majority of trees and shrubs do not bleed from wounds in the wood at any season of the year and that the few species in the latitude of Massachusetts which exhibit this phenomenon at all, do so to a considerable extent only when deprived of their foliage.

Of more than sixty species of trees and shrubs which Clark tested by boring a three-quarter inch hole usually to a depth of two inches into the sapwood near the earth, only those of the following genera showed any tendency to bleed: Betula, Acer, Vitis, Ostrya, and Juglans. These trees were tapped on March 10, April 21, and April 30. It was found that each species of those which bleed has its own time of beginning, that the flow steadily increases in quantity and force as indicated by the weight of the sap, amount exuded, and the pressure on the mercurial guage used, until its maximum , and then gradually declines, and that the composition of the sap of several species differs according to the date of the flow and especially the time of beginning. From these data he concludes that "the periodicity peculiar to every species demonstrates that the absorption of water by the rootlets is not caused by osmose, or any other mere physical force, but is the result of the specific life which imparts to every plant its distinctive characteristics".

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Clark finds the periods of sap flow to be: Maple, October to May, with a maximum in April; the black birch, from last of March to middle of May, with a maximum the last of April. The wild grape commences about the first of May and ceases early in June. The principal ingredients of maple sap is cane sugar while that of birch is grape sugar; that of vine, mucilage or gum. Clark thinks these carbohydrates are formed from starch after the period of spring activity begins, that cane sugar is formed only under favorable conditions, and that this transformation requires longer time, which accounts for maple being gorged with sap for six months. The spring sap of vine at the beginning of its motion about the first of May seems to contain no sugar of any kind, but three weeks later it often has a sweetish taste and may contain a trace of grape sugar.

By a careful comparison of the daily weight of sap from several trees with the meteorological observations of the same period, Clark concludes that the general flow corresponds with the seasonal changes rising to a maximum and then declining, yet the daily and hourly flow varies with the weather. The most unfavorable weather is that which is either steadily or severely cold or uniformly warm and foggy.

It is well known that sap flow in maple declines in the evening or with cooling weather. Freezing nights and sunny days are best for sap flow. Clark thinks the logical

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explanation for this is that the outer tissues of the tree are partially emptied of their contents by the contracting influence of cold, the sap being driven into the heartwood of the higher parts of the trunk. Meanwhile absorption goes on as usual in underground parts and thus, when relief is afforded by the expansive influence of the heat of the sun, the sap rushes to the surface and flows abundantly.

Clark says in his conclusions "we may as well admit that life is still a special force and not to be resolved into any other sort or combination of attractions or repulsions, whether called electricity, osmose, or any other name."

Detmer (13) believed with Hofmeister that root pressure is developed through the rapid intake of water through root cells, thereby becoming turgid and pressing the liquid through the vessels. In his experiments he found the optimum temperature for bleeding to vary with the species of plant used, varying from 25 - 27°C for Begonia incarnata to 43°C for Cucurbita Melopepo. He finds that the higher the water content of the soil the more sap will be exuded. It is also interesting to note that he finds that the birch will bleed at night and early morning after having its foliage developed. However, while transpiration is going on as rapidly, water is sucked in from a wound.

Concerning the periodicity of bleeding Detmer draws the following conclusions:

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1. Many plants show, when they have reached a certain age, that there is a definite periodicity of bleeding varying with temperature and moisture.

2. Very young plants do not show a definite periodicity.

3. Etiolated plants show no periodicity.

4. Plants that have been grown in a vapor saturated atmosphere do not show any periodicity of bleeding.

Detmer believes that the periodicity of the exudation bears a close relation to the periodicity of growth and transverse tension. The periodicity of growth is brought about through the change of temperature, moisture content of the surrounding air, and light changes, so he concludes that the same factors that control growth control exudation.

Pitra (45) conducted various experiments to determine the sap pressure in stem and roots. He points out that all previous workers attributed bleeding pressure to roots only. He conducted experiments with stems to see if they would bleed and if they would develop pressure. He experimented first with leafy twigs immersed vertically in water with the cut end protruding above the surface, to which a glass tube was attached by means of rubber tubing. Of eight plant varieties used, seven pushed water up into the tubes to various heights. This, according to Pitra, shows two new facts:- first, that leaves can take up water when immersed; and second, that stems can produce a pressure.

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Pitra's experiments with leafless twigs of birch show that pressure is developed depending upon the season. They show pressure in the spring but none in the fall and winter. A twig 575 mm. long develops a pressure of 302 mm. water.

Pitra compared the pressure of root and stem by cutting the plant off just above the soil and immersing both twig and root in water. Twenty-three species of plants were tested. Eight did not bleed either from root or stem. Only one showed bleeding from the root and not from the stem. Some bleed most from the root and some most from the stem. Hence he has shown that stems as well as roots can exude water and develop pressure.

In a series of elaborate experiments, Kraus (33) shows that twigs of almost any tree or herbaceous plant will exude sap from a cut end if immersed in wet sand. He also shows that there is no definite relation between the strength of the flow and the time it will continue. He finds that many different elements of the stem may exude sap, viz., parenchyma, sieve tube, fibers, collenchyma, and young wood cells, that the method of cutting makes no difference because it will bleed if cut tangentially, transversely, or any way to produce a wound. From his various experiments Kraus concludes that the exudation of sap is not a result of disturbance of the normal life processes of the plant, but rather a normal

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function of the living cells.

Wieler (62) has made the most thorough study of sap exudation. He repeated the work of previous investigators and added much more experimental data to the large amount at hand. He has collected a full list of plants that bleed from wounds with the name of the investigator who first observed them.

Name of Plant	Family	Name of Observer
Asplenium Ruta muraria	Filices	C. Kraus
Abies excelsa	Coniferae	"
" pectinata	"	Pitra
Cupressus funebris	"	"
" horizontalis	"	C. Kraus
" Lausoniana	"	Pitra
Pinus insignis	"	C. Kraus
" sylvestris	"	"
" strobus	"	"
" nigricans	"	"
" Pinea	"	"
Taxus baccata	"	Pfeffer
Thuja occidentalis	Coniferae	"
Thoa urens	Gnetaceae	Treviranus
Arum Colocasia	Araceae	Unger
Richardia africana	"	"
Calla palustris	"	Volkens

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Cocos nucifera and other palms	Palmae	Treviranus
Bambusa arundinaceae	Gramineae	Cohn
" stricta	"	"
" vulgaris	"	"
Zea Mays	"	Horvath
Poa pratensis	"	C. Kraus
Asparagus officinalis	Liliaceae	"
Agave	Amaryllideae	A. V. Humboldt
Iris pumila	Irideae	C. Kraus
Musa	Musaceae	Treviranus
Betula alba	Betulaceae	Clark
" lenta	"	"
" lutea	"	"
" papyracea	"	"
" (gray birch)	"	"
Alnus	"	Treviranus
Corylus avellana	Corylaceae	C. Kraus
Carpinus Betulus	"	Ray, Dutrochet
Ostrya virginica	"	Clark
Fagus silvatica	Cupuliferae	Dutrochet
Quercus Robur	"	Th. Hartig
" pedunculata	"	C. Kraus
Juglans regia	Juglandaceae	Ray, Th. Hartig
" cinerea	"	Th. Hartig

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Carya	Juglandaceae	Clark
" alba	"	"
Salix	Salicaceae	Ray
" alba	"	C. Kraus
Populus canadensis	"	Th. Hartig
" serotina	"	"
" tremula	"	Hofmeister
Urtica urens	Urticaceae	"
Morus alba	Moraceae	"
Cannabis sativa	Cannabineae	Horvath
Humulus Lupulus	"	C. Kraus
Platanus occidentalis	Platanaceae	Clark
Fagopyrum esculentum	Polygonaceae	C. Kraus
Polygonum Persicaria	"	Volkens
Chenopodium album	Chenopodiaceae	Hofmeister
Atriplex hortensis	"	"
Beta vulgaris	"	C. Kraus
Mirabilis Jalapa	Nyctaginiaceae	"
Spergula	Caryophyllaceae	"
Tetracera potatoria	Dilleniaceae	Treviranus
Menisperum canadense	Menispermaceae	Hofmeister
Papaver somniferum	Papaveraceae	Hofmeister
Brassica aleracea	Cruciferae	Horvath
Brassica Napus rapifera	"	C. Kraus
Raphanus	"	"
Bunias orientalis	"	"

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Lepidium sativum	Cruciferae	C. Kraus
Sinapis alba	"	"
Camelina	"	"
Cheiranthus Cheiri	"	Cohn
Tilia parvifolia	Tiliaceae	C. Kraus
Aesculus Hippocastanum	Sapindaceae	"
Acer-Arten	Aceraceae	"
Acer pseudoplatanus	"	Ray
" campestre	"	"
" platanoides	"	C. Kraus
Vitis vinifera	Vitaceae	Hales
" aestivalis	"	Clark
" cordifoliaria	"	Cohn
" Labrusca	"	"
Ampelopsis quinquefolia	"	Wilson, C. Kraus
Cissus hydrophora Gand.	Gandichaud	Gandichaud
Euphorbia	Euphorbiaceae	C. Kraus
Ricinus communis	"	Detmer
Omphalea diandra	"	Treviranus
Cornus mas	Cornaceae	"
Ribes Grossularia	Saxifragaceae	C. Kraus
Pittosporum Tobira	Pittosporaceae	Pitra
Begonia incarnata	Begoniaceae	Detmer
Fuchsia	Onagraceae	
Prunus Laurocerasus	Rosaceae	Detmer, Pitra

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Prunus avium	Rosaceae	Dutrochet
" domestica	"	C. Kraus
Pirus-Arten	"	Hofmeister
Lupinus angustifolius	Papilionaceae	C. Kraus
Phaseolus multiflorus	"	Hofmeister
Pisum sativum	"	"
Robinia Arten	"	"
Trifolium pratense	"	C. Kraus
Vicia faba	"	"
Virgilia lutea	"	Th. Hartig
Acacia leptophylla	Mimoseae	Pitra
" lophantha	"	C. Kraus
Ardisia crenulata	Myrsinaceae	Detmer
Petunia nyctaginiflora	Solanaceae	Hofmeister
Nicotiana tabacum	"	Horvath
Solanum tuberosum	"	C. Kraus
Datura tatula	"	Horvath
Digitalis media	Scrophulariaceae	Hofmeister
Alloplectus speciosus	Gesneraceae	Detmer
Fraxinus excelsior	Oleaceae	C. Kraus
Cucurbita Pepo	Cucurbitaceae	Detmer
" Melopepo	"	"
Sambucus nigra	Caprifoliaceae	C. Kraus
Siphocampylus lutens	Lobeliaceae	Pitra
Chrysanthemum coronarium	Compositae	Hofmeister

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Dahlia variabilis	Compositae	Horvath
Helianthus annuus	"	Baranetzky
" tuberosus	"	"
Lactuca	"	C. Kraus
Scorzonera	"	"
Sonchus oleraceus	"	Hofmeister
Galmsogea parviflora	"	Volkens

The term bleeding is used in this table in its narrower sense to mean the exudation of sap when the upper parts of plants are cut off. In this case the exudation strength is due to the root system. The list includes about 126 species of 93 genera of 47 families of filicales, gymnosperms, monocots, and dicots. To this table Wieler adds the ones he has found which had not been reported before. This includes some 62 species of 51 genera of 33 families, including some mosses.

Name of Plant	Family
Ceratodon purpureum	Muscineae
Bryum spec.	"
Mnium undulatum	"
Polytrichum spec.	"
Equisetum arvense	Equisetaceae
Cupressus Lindleyana	Coniferae
Picea Omorika	"
Pinus Lambertiana	"

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Elodea canadensis	Hydrocharideae
Caladium nymphaeifolium	Araceae
Alocasia cucullata	"
" odora C. Koch	"
Phoenix dactylifera	Palmae
Cyperus Papyrus	Cyperaceae
Triticum vulgare	Gramineae
Secala cereale	"
Oryza perennis	"
Allium Cepa	Liliaceae
Hyacinthus orientalis	"
Tulipa Gesneriana	"
Narcissus poetica	Amaryllideae
Aechmea fulgens	Bromeliaceae
" discolor	"
Eichhornia crassipes Salnis	Pontederiaceae
Eichhornia cezurea	"
Heteranthera renifornium R.& Pav.	"
Thalia dealbatus	Marantaceae
Canna indica	Marantaceae
Piper mollissinum	Piperaceae
Artanthe "	"
Laportea peltata G	Urticaceae
" gigas	"
Ceratophyllum	Ceratophyllaceae
Clématis alba	Ranunculaceae

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Adonis aestivalis	Ranunculaceae
Nymphacea coerulea Sav.	Nymphaeaceae
" rubra	"
Nelumbium speciosum	"
Hibiscus, alle Arten	Malvaceae
Impatiens glandulifera	Balsameneae
" Sultani	"
Acer californicum	"
" dasycarpum	Aceraceae
" Negundo	"
" rubrum	"
" talaricum	"
Cissus discolor	Vitaceae
Bryophyllum calycinum	Crassulaceae
Ribes rubrum	Saxifragaceae
Hydrangea hortensis	"
Begonia platanifolia Schott	Begoniaceae
Myriophyllum proserpinacoides Gill & Hook	Halorrhagidaceae
Hippuris vulgaris	Hippurideae
Lycium flaccidum	Solanaceae
Coleus	Labiatae
Columnea Schiedeana	Gesneraceae
Aphelandra micans	Acanthaceae
Cyrtanthera magnifica	"
" Pohliana	"
Schaneria calycotricha	"

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Syringa vulgaris	Oleaceae
Gynura aurantiaca	Compositae

Wieler was the first to observe the bleeding of mosses. he found if he cut Mnium undulatum off in a saturated atmosphere drops collected on the cut end. Polytrichum acted the same. The capsule petiole or stalk of Ceratodon and Bryum shows active bleeding if cut. However, the stalk of Marchantia did not show any bleeding. Equisetum bleeds from both fertile and sterile branches.

Wieler's experiments with phanerogamic land plants were conducted mostly with potted plants. These were kept in a constant temperature room to determine whether or not temperature had any effect. After the plants had been thoroughly watered they were allowed to stand in a saturated atmosphere under a bell jar so they would become constant in temperature and so that they might become thoroughly saturated. After they were cut off a beaker was placed over the stump to prevent excessive evaporation from the cut surface and the bell jar was then placed over this.

Wieler tested water plants to see if he could induce bleeding. These were tested in an aquarium in the greenhouse. He tested those which are not completely submerged by cutting off the stem just above the water. The table above shows those that bleed. Submerged plants such as Elodea and

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Ceratophyllum were tried in the laboratory. They were tested by hanging them in a vessel with a part of the plant above water. The part was cut and the vessel in which it was immersed was covered with a glass cover so that the part of the plant above water was in a saturated atmosphere.

Wieler points out that not only the higher land plants but water plants, mosses, and also fungi possess the power of bleeding. He states that there are many conflicting results found concerning many species. Thus one investigator will report bleeding for Conifers while another will deny this. Some have found variation within the same species. Hartig (24) found individual differences in Quercus. Nördlinger (41) found similar variations. Wieler compared like individuals under like surroundings and found great differences both in amount of sap exuded and in the pressure developed. He notes that this is important in solving the problem of bleeding because one can not experiment on two plants and get accurate results.

Wieler gives a list of about 300 species of 103 different families of plants which exude drops from intact leaves. I will not include this list since it does not bear directly upon the subject under consideration.

The question as to which parts of the plant are capable of bleeding is fully discussed by W ieler. He shows where many investigators have drawn inaccurate conclusions because they have experimented with two different plants of the same

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species. The amount of water exuded can depend only upon the pressure developed in the plant. This varies with each plant, hence Baranetzky's results above referred to are not trustworthy.

As has been shown, various investigators find that stems will bleed. Böhm (5) thinks this is due to pathologic conditions holding that when these twigs are immersed in water the supply of oxygen in the vessels is lowered to such an extent that intramolecular respiration ensues and carbonic acid is formed followed by the formation of butyric acid. Böhm holds that when these gases expand they drive the water before them and naturally it must be pressed out of the vessels. Wieler does not agree with Böhn for he says if carbonic acid is formed it would kill the twig and Böhm says in his article that twigs may adapt themselves to the water habit and live for a long time. Wieler thinks the butyric acid odor is due to decaying wood.

Not only can the stem bleed but, as has already been shown, leaves have this power. Wieler repeated Sachs' (52) experiments with monocot leaves such as Panicum, Zea, Triticum vulgare, and Secale cereale, with positive results. If these leaves are partly covered with wet sand with the cut end protruding and kept in a moist dark chamber they show active bleeding.

Wieler carried out extensive experiments with roots to

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see if all parts of roots are capable of bleeding and also to ascertain if age has any effect. The results show that all parts of the roots have the power of bleeding. If the upper part of the root doesn't bleed it means that there is a break lower down which is taking away the surplus liquid.

Having established the fact that all parts of the plant are capable of bleeding, Wieler takes up the question as to which tissue is actively operative in this phenomenon. All workers are agreed that active bleeding must be due to the active activity of living cells. The secondary wood and the primary vessels should have the power of bleeding because of their water content. The medullary rays must have because conifers bleed. The water in the vessels and tracheids of twigs of tall trees must be forced in from the living cells. The roots could not force water into the upper limbs of tall trees because the root pressure would not be felt at such a height. The water might collect by condensation but this would not account for the large amounts found. According to Hartig (24) a birch at 10 meters height has the following water content:

March	75%	September	47%
May	85%	October	39.5%
July	66.5%	December	29%
August	51%	February	41%

The amount of water which is necessary to bring about a full saturation with water vapor in a 100 cc. space with a

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rise of temperature from 0° to 30° is only 1/2 gram. This, as we see, is very low in comparison with the lowest water content of the cells above. Wieler points out that the high water content in the dead cells of the wood cannot be due to condensation and that it must be due to the pumping or bleeding action of the living cells. He thinks that bleeding may be a normal function of the living cell.

Kraus (34) states that he finds active bleeding from all parts of the stem. Hence according to this view the pith, cambium, collenchyma, woody cells of xylem, and bark cells are all capable of bleeding. Wieler does not agree that all cells may function thus. He rather thinks there are specialized cells which have the power of pressing out water from one side and that this power is not possible for all cells. He seems to think that the main seat of bleeding is in the wood parenchyma.

The relation of bleeding to external factors is fully discussed by Wieler. He first considers the relation of moisture to bleeding. Earlier workers, as we have noted, found that moisture had a great effect on bleeding. Brosig (6) believes that increase in bleeding, if the soil is flooded with water, is due to little spaces in the soil which are filled until flooded. Wieler thinks if this were the case the rise in sap pressure would come at once instead of two to four hours as is actually the case. Wieler also finds that if plants do not show bleeding in saturated soil, they

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can be induced to bleed by transplanting into a solution and thinks this may be due not to an increase of water surface on the roots, but to wounding of the roots in transplanting. This would wound the corky layer and might enhance the entrance of water.

The salt concentration has an effect on the bleeding as well as the water content of the soil. Very weak solutions even effect the intensity. Brosig (6) and Detmer (13) find that bleeding is stopped and water may even be pulled in from a tube connected with the stump if the roots of the plant are immersed in a salt solution. Wieler finds that the concentration which will stop bleeding depends upon the osmotic power of the solution, a 1% solution of KNO_3 and a 2% solution of glycerine will inhibit bleeding, while a 2.8% solution of gum has no effect. If, however, plants are left in solution any length of time they will accommodate themselves and continue in time to bleed normally. However, he finds that a 10% solution of KNO_3 was too strong for this adaptation. If the plant is brought from a 10% solution to a 5% solution, it may bleed.

Since bleeding is dependent upon osmotic pressures, temperature must play an important role. Hofmeister (25) noted bleeding of a grape vine at 1°C. As has been noted maple may bleed during a mild winter. Wieler noted Juglans showed active bleeding in February. I have noted during

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wood chopping season that walnut trees will bleed in January in the central states even while the ground is frozen. In one instance in Kansas there was from six to eight inches of ice on the stream nearby but the exudation was very active and sap ran almost the length of the tree when a cut was made. Wieler's work with potted plants show so much individual difference and so much difference between species that he could not state any definite temperature minimum. Vitis vinifera bled in a water culture at 7.6°C. Acer platanoides bled between temperatures of 0° and 2.6°C.

Wieler finds the same difficulty in establishing a rule for the maximum as for the minimum temperature. Usually bleeding stops between 38 and 40°C. Salix alba, Populus canadensis, Betula alba, Ampelopsis quinquefolia, Ribes rubrum, Abies pectinata, Alnus glutinosa, and Acer platanoides show a maximum between 35 - 40°C.

Of much greater importance is the optimum temperature for exudation. Detmer found an optimum of 25 - 27°C for Begonia incarnata and Cucurbita Melapepo. Wieler finds that Vitis vinifera gave off eight times as much sap at 38 - 40° as at 8°C. His results seem to indicate that there is a definite optimum, at least that there is a great difference in the amount exuded at various temperatures.

By experimenting with closed vessels and circulating hydrogen through them, Wieler showed that oxygen was absolute-

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ly necessary for bleeding. The plants were tested at first to see if they showed bleeding. The current of hydrogen was continued until all oxygen was removed. Then after the bleeding stopped, oxygen was again run through and the plant began to bleed.

The effect of an anesthetic was tried by Wieler. Chloroform with a concentration of 1 to 6 of water did not stop the bleeding of Zea Mays, but a 1 to 4 solution was strong enough to stop active exudation. A 1 to 3 concentration stopped the bleeding of Secale cereale. He finds the same results with other plants. This effect of an anesthetic he thinks shows that bleeding is not a chemical oxidation process but that it is dependant on the influence of protoplasm.

Wieler finds the effect of gravity to be quite variable. With Alnus glutinosa a decided increase in bleeding was noticed when the plant was inverted. With birch the opposite results were obtained. Hence he says it is not possible to draw any definite conclusion. The earliest workers noted that plants showed a yearly periodicity. In northern Germany the birch begins to bleed in early March. In the Rhine region the walnut begins early in February. In England the grape bleeds from March 10 to the last of April. Hartig (24) observed oaks bleeding in August. According to Nördlinger (41) some trees may bleed in November. He observed the hornbean bleeding when the leaves were half mature. I have

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noted the maple bleed when the leaves are half mature when transpiration is checked. Binx (4) states that one can only prune walnut trees when they are bearing fruit. These observations were made in the open. If one wants to determine if there is an inner cause of periodicity, he must do away with temperature and soil changes. W ieler carried out experiments in the greenhouse where he could control soil temperature, water content, and outer temperature. The experiments were conducted at a temperature of 19 to 20°C. The following species were tested:

Vitis vinifera	70	examples
Ampelopsis quinquefolia	75	"
Ribes rubrum	66	"
Salix alba	40	"
Populus canadensis	55	"
Lycium flaccidum	58	"
Abies pectinata	47	"
Fraxinus excelsior	20	"
Acer platanoides	35	"
Betula alba	47	"
Alnus glutinosa	17	"

No bleeding took place for

Populus canadensis from end of July to May 1,

Fraxinus excelsior from August to April,

Ampelopsis quinquefolia from November to April,

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Lycium flaccidum from November to April,

Salix alba from November to February,

Ribes rubrum from November to December,

Betula alba from November to December,

Acer platanoides November only,

Vitis vinifera from January to February.

Wieler believes the above results show that there must be some factor or condition in the cells which determines when the plants shall bleed. During the period of rest these conditions must not be fulfilled or present. There must be a bleeding condition and a non bleeding condition.

Wieler found that he could change the regular bleeding period by bringing plants from the outside into the greenhouse and thereby shortening the resting period. He experimented with plants which have a sharply defined bleeding period, such as Vitis vinifera, Ribes rubrum, Alnus glutinosa, and Betula alba. He also varied the regular bleeding period by treatment of roots with a weak osmotic solution such as glycerin, sugar, KNO, etc. A very weak concentration does not bring about bleeding. However, if the solution is too strong, no bleeding results. A solution within definite limits of concentration is necessary.

To test the effect of temperature he first subjected plants during the winter months to a constant temperature of 19°C to see if they showed bleeding. They were then

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subjected to a temperature of 37 - 39°C. The results showed that temperature changes can bring about results which in nature are brought about by other means. Of 27 samples tried, only 6 did not bleed. This high temperature brought about the unfolding of the buds also. It is a question if bleeding is the primary thing and unfolding of the buds secondary or the reverse.

Scheit (54) was the first to observe that if plants which did not bleed were attached to a suction pump, bleeding might be induced by emptying the vessels. The twig was cut and fastened to a glass tube with rubber tubing and the glass attached to a water pump. Wieler repeated these experiments and found that he could induce bleeding of examples of Quercus and Lycium by this method. The bleeding continued after the pump was detached. No explanation is offered for the phenomena except that it may be due to the lowering of the resistance through pumping out of the Jamin chain and thereby making it possible for the pressure to suffice to force the water out.

Wieler's conclusions from these and the preceding results are that bleeding is dependent upon certain conditions in a living cell. These conditions are reached only in certain periods of the year and are not present during the rest period. In spring there may be a metamorphosus of material which brings about high pressure. By varying the

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natural condition of the plant these changes may be brought about artificially. Just how the changes are brought about he does not know.

Wieler takes up the relation of root formation to periodicity and notes that Resa (48) found two periods of root formation: one before the formation of shoots, and the other late in the summer. Wieler did not find root formation in fall or early winter. He did find that roots were usually formed before the plant showed signs of bud formation. In case of Populus, Salix, and Ampelopsis there seemed to be a relationship between root formation and bleeding pressure, however it is not safe to say that bleeding is dependent upon root formation as the conditions for bleeding in some species may be met without root formation. The age of the root seems to have no effect upon bleeding for he found that bleeding from a four year old birch corresponded very closely with that from young plants.

Wieler also measured the quantity of sap given off at different periods. He found the greatest amount for Betula in March, for Vitis in May, for Juglans in February. These results are not very striking because of so much individual differences in plants. This difference he thinks is due to the number of cells concerned in the bleeding.

The following table taken from Wieler's results shows the yearly periodicity of the bleeding pressure of Betula

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alba.

Oct. 21, 1890 - 50 mm.	July 7, 1891 - 28 mm.
Jan. 21, 1891 - 99 "	July 10,1891 - 95 "
Feb. 24, 1891 - 494 mm.	Aug. 3, 1891 - 405 "
Apr. 16, 1891 - 240 "	Aug. 4, 1891 - 244 "
Apr. 21, 1891 - 366 "	Mar. 18,1892 -1038 "
	Mar. 21,1892 - 557 "

The differences in the above table are so great that Wieler thinks they cannot be due to individual variations; hence he does not agree with Hofmeister that the pressure is fairly constant. The maximum seems to be in spring. He found the definite maximum for Vitis to be in May. From the results of the bleeding pressure and the amount of sap exuded, we can conclude that there is a definite relation or parallelism between them.

Using Pfeffer's (44) modification of Baranetzky's apparatus for registering the amounts of sap exuded at different periods of the day, Wieler found that the maximum was usually reached in the afternoon.

The mechanics of bleeding is fully discussed by Wieler, He points out that the earlier workers attributed bleeding to osmotic processes and tried to demonstrate these by means of physical experiments but did not succeed in showing how there could be a continuous stream of water from the cell. Pfeffer gives as a possible theory a one-sided loss of water in the cell by tissue tension, but does not believe that

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this can account for bleeding, since we could not account for a continuous stream of water by this means. Wieler agrees that there is negative tension in the tissue which increases from the wood out to the periphery. The question is under what conditions water can be pressed out by this tension. There is transverse as well as longitudinal tension. In case of the transverse tension we might consider a wooden cylinder of two cells thickness for example. The intensity of the tissue may be varied in two ways: 1st, through the contraction of the outer layer which would produce a pressure on the inner; 2nd, the tension of the inner layer may be lowered by taking up water, thus raising the tension of the outer. The first would account for the exudation of water because the tension of the outer layer would produce pressure on inner and hence bleeding. In the second no water would be pressed out; however, the outer would be under greater tension. It is questionable which of these are active in the plant. If there is active bleeding the first must be active. From Krabbe's (32) work on the tangential tension of bark of older trees, we might conclude that the radial pressure due to the tissue tension on the cells may reach 1/3 to 1/2 atmospheres, but as the tissue tension is not altogether released we can only figure on a part of 1/3 to 1/2 atmospheres. This amount is too small to be of much value in accounting for bleeding. The amount of exudation would depend

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upon the difference between the minimum and maximum tension, hence it would be necessary for the change to take place very rapidly. This does not occur. Wieler thinks, however, that the maximum and minimum tensions may have something to do with maximum and minimum exudations. Another argument against tissue tension as a bleeding factor is the bleeding of young roots which do not develop much tension. Nor could we account on this basis for bleeding in trees which have had the bark removed. Therefore Wieler says it remains to attribute bleeding to the action of living cells and to find out the mechanics of their action.

Sachs (51) was the first to explain bleeding as due to individual cells. He believed that bark cells of the roots in the periphery and central parts possessed cell walls of peculiar nature whereby water would be taken up on one side and passed out from the other side. Thus the cells act like a suction and pressure pump. When Pfeffer demonstrated the existence of a plasma membrane Sachs substituted plasma membrane for cell wall in his theory.

Pfeffer (44) has stated the condition under which it is possible to have a continuous water stream through a cell. The necessary condition is fulfilled: 1st, when there is a difference in permeability of the plasma membrane on opposite sides of the cell; 2nd, when there is equal permeability of the plasma membrane but when there is a greater concentration

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of osmotic substance on the plasma membrane on opposite sides of the cell; 3rd, when there is equal permeability and equal concentration of osmotic substances in the plasma membrane but the cell wall contains osmotic solutions of greater concentration on one side of the cell than on the other side.

Wieler discusses at length the possibilities of Pfeffer's first theory. He says that if bleeding is due to the difference in permeability, there must always be a fairly high osmotic concentration in the sap, for if the membrane is fairly permeable on one side of the cell the osmotic substance would pass through with the solution. In the maple and birch this theory could hold because the sap exuded contains enough osmotic substance to account for the pressure, but in some plants the sap exuded is almost pure water and we could not account for such high pressures as are developed unless the osmotic substances are used by the cell and are not exuded with the sap.

According to the researches of A. Fisher (18) there is glucose present in the maple all winter and, as we have seen, Wieler found the maple and birch could be induced to bleed during the greater part of the year. This phenomenon would work in very nicely with the permeability theory. Wieler thinks the character of the sap exuded excludes the possibility of unequal imbibition due to osmotic substances in the cell wall. He showed by experiment that this unequal

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distribution of substances does not bring about bleeding. By fitting a glass tube on a decapitated stump and adding a weak salt solution he brought about the condition of unequal distribution of osmotic substances as the cell walls imbibed the solution. Of eleven tests none showed bleeding.

Wieler thinks there is a possibility of the difference of concentrations in the plasma membrane. He refers to Klebs' (30) work on the plasmolyzed protoplasts of Zygnema. Klebs found that, if Zygnema was kept in a sugar solution, the short walls of the cells grew faster than the long ones. In some cases the plasmolyzed protoplasts grew faster at one end than at the other. In that case there would be a difference in the opposite ends of the cells which eventually would make a difference in the amount of the osmotic pressure. Because the growth of the protoplast is dependent upon the interchange of substances in the cell, Wieler concludes that it is altogether probable that under certain conditions the plasma membrane on one side is built up in a different manner than on the other and that this can account for a flow of water through the cell. He thinks there might very well be a combination of methods. Thus as in certain fungi, the loss of water from sporangiophores might be due to a difference in osmotic substance in the cell, but when the drops collect on the points of the hyphae, the osmotic substance of the droplets might be imbibed by the wall, thus increasing the

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osmotic powers of the drops. Or the liquid on the outside of the wall might become concentrated through evaporation so as to bring about an outflow of water.

Wieler's final conclusions on the mechanism of bleeding are:

1. That bleeding is an attribute of certain cells.

2. It is brought about by unequal distribution of osmotic substances on opposite sides of the protoplast.

3. In conjunction with this action there may be an action due to exosmosis of osmotic substances and partial imbibition of the cell wall due to exuded osmotic substances.

4. In any case the plasma membrane is concerned as bleeding requires the presence of oxygen.

The most extensive work done by Americans on the bleeding problem was done at the Vermont Experiment Station by Jones, Edson, and Morse (29). Their work is a specific investigation of the flow of sap in the maple tree and bears a direct relation to the maple sap industry. Some of the problems which they investigated were: the source of the sugar, the relation of tree structure and its life processes to sugar storage and transfer, cause of sap flow, relation of sap flow to meteorological changes, water and gas content of tree variations, pressures within the tree, temperature, etc., relation of the flow to the location of the tree, and the extent and cause of variation of sap flow.

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Jones and co-workers first take up the general structure and physiology of the maple tree. Among other things they point out that the maple contains a larger amount of sap wood than most trees. A tree thirty inches in diameter has, for example, an average of six inches of sapwood. The sapwood is the conducting tissue while the heartwood is composed of closed cells and vessels packed closely together with no intercellular spaces, such as occur in the stem of some species of plants. The ingredients of these cells are water, starch, sugar, and gas. It is found that the sugar content of the sap depends upon the condition of the preceding seasons as to sunlight and leaf development. The evidence for this is apparent as defoliation of the trees by caterpillars was always followed by seasons in which the sap carried much less sugar than normally was the case.

The excess of these carbohydrate foods gathered during the immediate needs in summer months is stored for use in the early growth of the following spring. Studies by Spaulding and White of the Vermont Station show that this storage occurs chiefly in the cells and fibers of the sapwood, viz. in the medullary rays, parenchyma, and the fibrous cells. The fibers may be packed full of starch but this has been found only when the other starch containing tissues were very rich in starch and then only those fibers lying in close proximity to the medullary rays which were filled. This

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indicates that these fibers are filled last of all. Apparently the medullary rays are the first cells in which the starch is stored. The pith does not contain starch unless the rays and outer cells are full. It seems then that the starch is stored in the outer cells first and thence progressively inward. In the spring the starch disappears from the outer cells first and then progressively disappears toward the center.

Microchemical tests show that with the disappearance of starch the sugar content of cells increases. When a branch is cut in mid winter and kept for some time in a warm room, these same changes are observed. The transformations are controlled by the protoplasm and are brought about by the action of ferments.

The terminology used by these investigators conforms with that of Peirce (42). They distinguish between "sap pressure" and "turgor pressure". They use the sugar maker's term of "running" instead of "bleeding". The term "sap movement" is used to designate the movement of sap from other parts of the tree to the point of escape, i.e. to the tap hole. This movement is so closely correlated to the "running" that they use the term "sap flow" to include the two phenomena in a general way.

The water content of the tree was taken for three successive years. A comparison of the outer and inner

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tissues show on December 13, 37.5% for the outer and 24% of water for inner tissues. From this time until March 11 the water content of the outer tissue decreases and that in the inner wood increases so that on the latter date the outer wood contained 33.4% and the inner 39.1% of water. From March 11 the amount of water increases in both tissues, and then for a week there is a rapid decrease in amount of H_2O, both decrease and increase being greatest in the inner tissue. After June 9 each tissue contains nearly the same amounts.

It appears that the outer few inches of the sapwood are the first to be highly charged with water in winter and early spring, but that upon renewed activities these same tissues are the first to show reduced water content. The seasonal variation may reach as high as from 27% in December to 47% for April. However, the greatest sap flow does not take place when the tree has the highest water content. Hence sap flow is not directly dependent upon the water content.

Water contents of other trees compared with Maple.

	April 8	May 1	May 23	Av.	Change
Maple	38.8	30.8	28.5	32.0	-10.3
Ash	42.0	42.3	39.9	41.4	- 2.7
Beech	37.9	42.8	44.5	42.0	+ 6.6
Birch	41.8	61.4	66.2	56.5	+24.4
Butternut	37.8	42.4	45.0	41.8	+ 7.1
Elm	45.4	44.9	38.4	42.9	- 7.0
Hornbeam	44.4	55.8	37.8	45.8	- 6.5

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The Vermont people account for the variation in the water content by the variation in the time of leaf formation. The maple and elm form leaves earlier than other trees.

The gas content (determined by Sachs (51) method) is given as compared with the water content.

Date	Percent of cell wall structure	Percent of gas	Percent of water
April 30	41.1	24.0	34.8
May 5	34.9	20.8	44.4
May 12	31.1	25.8	42.1
May 19	36.1	23.3	41.7
May 26	36.0	29.4	34.7
June 2	32.2	24.7	39.2
June 9	35.7	25.5	38.8
June 16	36.5	21.2	42.3
June 23	38.1	25.6	36.3
Average	36.4	24.4	39.4

The above table shows in general that the water and gas contents varied inversely to each other. If temperature changes are rapid differences in tension in different parts of the tree may arise. During the greater part of the year the pressure within the cells is less than that of the atmosphere, hence the gas is in a state of suction.

Jones' and co-workers experiments concerning the relation of pressure and suction at different times in the year show that from January to mid March the tension is almost nil. Then great oscillations in pressure, which are characteristic of the sugar season and which are closely related to the sap flow phenomenon, set in to continue until the buds begin

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to swell. The pressure in trees was investigated for a period of five years. Self recording dial gauges were found to be the most satisfactory instruments for measuring the pressures.

The pressures fluctuated with the temperatures. If the nights were warm running might continue all night. A direct relation between temperature and pressure was shown by gauges on trees located on slopes where the tops of trees were exposed to the morning sun before the lower parts were. In this case the upper set of gauges showed pressure before the lower set.

The internal conditions favoring sap flow develop in different parts of the tree at different times. They occur first in the twigs and branches and in the external layers of the wood of larger branches and trunks, passing gradually to the deeper tissue and lower parts. The reversal of these conditions occurs in the same order. Comparative pressures at different depths show the following results. Both pressure and suction are greater in the outer than in the inner tissue until late in the season. The outer tissue respond more quickly to temperature changes than the inner ones.

The downward, upward, and sidewise pressures were taken with specially constructed apparatus. The results show a difference between downward and upward pressures. The

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pressure in any given tap hole is a result of the combination of the two pressures. Early in the season and on good sap days throughout the season the greatest pressure is downward and on poor days and late in the season the pressure is from below upwards.

Jones, Edson, and Morse conclude that because good sap days are preceded by heavy frosts, the temperature has developed strong negative pressure in the trunk of the tree and has caused a movement of sap from the roots into the trunk. This sap is then distributed in proportion to its mass. With a sudden rise of temperature above zero ($32^{\circ}F$), pressure develops and it develops most quickly in those parts most quickly warmed. These conditions would lead to a stronger pressure from above downwards.

Experiments to measure the transfer of pressure by releasing gauges at different heights show that a ten pound pressure may be transferred a distance of eight feet. They could not transmit pressure laterally however. Hence they conclude that pressure must be transmitted through the tracheae.

Experiments with lithium chloride show the rate of movement of sap to be from 2 to 6 inches per minute. No sap was exuded with negative pressure but at zero or a little above sap began to flow.

The writers discuss several possible theories to explain their results. The gas expansion theory of Sachs

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(51) fits in very nicely with the observed facts that the stems always contained both water and gas and that woody walls like those under consideration are readily permeable by liquids like the cell sap but practically impermeable to gas. Under these circumstances changes in temperature could make great differences in pressure and also in exudation. They, however, show that according to the law of the expansion of gases the pressure developed with a change of temperature from 0°C to 27.3°C can only be 1.1 pounds per square inch. Their results show an extreme fluctuation of 31 pounds. Another argument against a physical explanation is the sudden cessation of flow at the end of the season while there are still temperature changes, and when the tree has the highest water content found during the year.

The bleeding of living cells has been discussed in connection with Wieler's work. The Vermont people think that the bleeding of living cells is the only plausible explanation for sap exudation. Variation of water content and temperature may account for minor fluctuation but cannot for the larger phenomena. They explain the suction or negative pressure as being due to reabsorption by the bleeding cells of the sap exuded by them into the vessels, in which case it may be regarded as an osmotic phenomenon due to changes in sugar content.

Evidence from the observations of the above named

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investigators lead them to the conclusion that bleeding is a normal process. They think there is a possible connection between the higher pressure and the maximum water content with leaf formation. The flushing of cells just before leaf formation may be a means of precaution against drying winds when the leaves are being formed as it is well known that at this stage the tree cannot guard against excessive transpiration as well as after the leaves are matured.

Wiegand (61) gives a detailed discussion of the work of Clark and of the Vermont Station. He discusses all the possible theories, viz. gas expansion, water expansion, wood expansion and the freezing theory, and concludes that we cannot account for maple sap flow without falling back on the theory of the action of living cells.

Wiegand would make a division of bleeding trees into two classes or groups: those which bleed early in spring, and those which bleed only later. The first class, of which the maple is an example, shows a definite periodicity and a sensitiveness to meteorological conditions. The second class, of which the birch is a type, show a gradual increase of flow until a maximum is reached and then a gradual decline. These are not susceptible to environmental factors in the degree that the trees of the first class are. The pressure in the birch is steady and the flow is quite regular. He thinks the trees of the latter class bleed

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mainly due to root pressure while in the trees of the former the bleeding pressure is developed mainly in the stem.

Lepeschin (36) conducted a series of experiments on the bleeding of the fungus Pilobolus. He states that former work has failed to establish a workable theory due to the fact that the investigators were dealing with many celled plants and did not locate the real source of bleeding. As is well known ~~that~~ the sporangial hyphae of this plant exude water which collects in the form of drops on the surface, Lepeschin tested the effects of different stimuli to prove which of the various theories of bleeding can account for the phenomenon. He was able to measure the amount of water exuded by using a micrometer in the ocular of the microscope. He also measured by collecting the exudate in capillary pipettes. The water seemed to collect at the same place at regular intervals. Drops of .2 mm. diameter were taken at intervals of 7-12 minutes.

Lepeschin found that the plants will not bleed in dry air. When plants are placed in osmotic solutions bleeding will be inhibited, but if the solution is not too strong, the plant will accommodate itself to the change. Bleeding increases with temperature up to 37°C, at which point growth is stopped. As has been shown, other experimenters found that higher plants will not bleed in oxygen free surroundings. He, however, found that Pilobolus will continue to bleed if grown in nitrogen. Anesthetics and poisons had

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varying effects. If used in quantities of less than 0.1 grams in 100 cc. air, an anesthetic such as chloroform or ether stopped bleeding. Any amounts above that increased bleeding. Other compounds such as NH_3, alcohol, etc., may be substituted for these anesthetics. Caffeine was also used. Direct sunlight inhibited bleeding, but diffuse light had no effect. He found that young cells bleed at the tip of branches while older ones may bleed all along the branch.

Lepeschin discusses the possibilities of the theories which have already been discussed above and concludes that the observed phenomena can be explained by the unequal permeability of the cell walls. To test this out he immersed the lower part of the plant and left the upper part free. He found that the sporange grew to normal size under such conditions. Then he reversed the process and immersed the upper part and left the lower part free. The relative growths of the sporanges in the two cases were 46 to 12. Respiration does not affect growth and bleeding. He showed that gravity has no effect for he grew the plants upright and enclosed upper parts with wet paper. Hence he concluded that the lower side of cell must function as water intake and must be less permeable. To test this further he enclosed the upper part as noted and exposed the lower part to chloroform. If the chloroform had had the effect noted before, the lower part would bleed and the upper would take

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in water. Instead the cell volume decreased a third and no bleeding resulted. Hence the upper part of the cell must be more permeable than the lower part.

Other plants were used as Phycomyces nitens, Mucor mucedo, and Vaucheria with the same results. By removing the water as it gathered and washing the surface he was able to show that the outflow was not due to a gathering of osmotic substances on outside of the cell. He experimented with hair cells of Phaseolus muliflorus and proved that the exudation was not due either to a gathering of osmotic substances on the outside of the cell or to constant renewal of osmotic substances in the plasma membrane. The concentration of the cells as shown by plasmolysis did not remain constant. The permeability of the plasma membrane for osmotic substances as well as for water was found to be greatly varied by internal and external changes. He is not certain whether or not these changes can be applied to all membranes. His conclusion is that one can not be certain that exudation is a physiological or only a physical phenomenon.

Merwin and Lyon (37) made many observations and determinations of the sap pressure of the birch. Their work checks up in most details with the work of Clark (9) and of the Vermont Station. They made observations of sap pressure as to seasonal and temperature variations and of different parts of the tree. In direct contrast to

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Wiegand's (61) work they found the pressure oscillations due to temperature to be much greater in the birch than in the maple. Their pressure curves show this very distinctly. From their calculations and observations they conclude that the two chief pressure producing agencies in the birch stem are root pressure and thermal expansion. The combined maximum pressure from the two comes at mid-day and the minimum at sunset. They think the maximum is about twice as high as if it came from root pressure alone.

Schaposchnikow (53) did some experimental work on the relation of water content of plants to bleeding. He experimented with Betula, Fuchsia, Dahlia, Geranium hybrid and haederifolium. In one case he kept the plant thoroughly saturated for at least 24 hours by wetting the soil and keeping the top covered. In the other he allowed the plant to stand in the open for several hours to bring about a loss of weight of 15 to 20%. At the end of these periods he decapitated the plants and measured the sap exuded from both kinds, trying to use similar plants for each comparison.

The results of this experiment were quite striking. If the trials were conducted as in the first case, with the plants fully saturated so that there was no falling off of pressure in the vessels, the bleeding curve was characterized by a gradual decline after the beginning of

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bleeding; if on the other hand, there was suction at the time of opening of the vessels, the bleeding curve was markedly different. The curves varied somewhat for different plants. They were characterized by the following generalization: bleeding begins with a strong suction which lowers quickly; with this lowering the bleeding increases with varying speed until it reaches a distinct maximum; from this point the curve takes a gradual drop. Schaposchnikow considers the bleeding curve as the sum of the two curves from which the one shows nothing but a regular outflow which is the case if the plant is fully saturated when the exudation begins, while the second shows a gradual rise to a maximum and then a decline.

S. Eckerson (16) has determined the amount of exudation and the pressure for a number of greenhouse plants which are usually available. She finds that Begonia, Geranium (Pelargonium), Helianthus, and Fuchsia show fairly high pressures and are suitable for experimental work. The mean root pressure found for 22 plants was .9 atm. She finds that Senecio Petasitis gives off the largest amount of sap, the amount being 110 cc. for 14 days.

S. M. Babcock (1) in a paper on the "Role of Metabolic Water in Vital Phenomena" discusses the possibility of carbon dioxide playing an important role in bleeding phenomena. He points out that according to A. Seidell's

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tables for the solubility of carbon dioxide at 0°C., water dissolves one and seven tenths times its volume of carbon dioxide, which is thirty-five times greater than the volume of oxygen and seventy times greater than the volume of nitrogen dissolved at the same temperature. However, at 30°C water only dissolves sixty-six hundredhts times its volume. Carbon dioxide is given off in respiration, therefore it must be present in fairly large quantities in the cell sap. Babcock believes that the influence of temperature upon the evolution and solubility of carbon dioxide is sufficient to explain sap pressure in the maple and other plants which exhibit these phenomena in early spring. A discussion of the possibilities of this and other theories will follow the discussion of the special problems of elm bleeding.

III. SPECIFIC PROBLEMS OF THE ELM

The general phenomenon of the bleeding of elm trees has not been observed to any great extent. Some of the investigators mentioned in the historical review did some experimental work and made some observations but their efforts were confined mostly to maples, birches, etc, which show a more active exudation. Clark (9) did not include the elm among bleeding plants, nor does Wieler (62) include it in his list. Wiegand (61) includes it among his second

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class of tress, namely those which bleed late in spring. No one seems to have made a study of the peculiar periodicity of the elm nor of the cause of its bleeding. From all general observations the bleeding seems to come from either of two places: from the crotch or fork of the tree, or from old sawed off limbs. I have seen holes in the bark of elm made by woodpeckers or by bark borers which in other trees would exhibit active exudation but which do not affect the elm. It would seem that bleeding comes from deeper tissue in the elm than in other trees.

1. Distribution of elm trees.

The elm is a widely distributed tree, being found in the eastern half of the United States and over the greater part of Europe. Brush (8) gives the distribution of the white elm Ulmus americana as the eastern half of the United States, taking in a part of Colorado, Montana, and Texas, including also the lower part of Canada. The slippery elm, Ulmus fulva, region does not extend quite as far west taking in only a part of North Dakota, South Dakota, Nebraska, and Kansas. Neither does it extend as far into Canada, nor completely to the coast of the south and southeastern states. The cork elm, Ulmus racemosa, includes in its range only the central part of the eastern half of the United States. It includes a part of the great lakes region and embraces the central part of the eastern half of the United States.

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The region of the winged elm, Ulmus alata, includes the southeastern quarter of the states with the exception of the tip of the Florida peninsula.

The elm is utilized to a great extent as a shade and street tree. For this purpose the white elm is much more desirable as the red elm has a very sparse foliage. Elm lumber, while not used extensively for rough building, is utilized to a great extent in the manufacture of boxes, baskets, vehicles, chairs, trunks, etc. The elm lumber industry has assumed quite an importance in Wisconsin, Michigan, and Minnesota. A total of 365,000,000 feet, board measure, is consumed annually in the United States.

2. Local distribution of bleeding phenomena.

During the two years in which I have observed bleeding phenomenon, I have been able to compare different local regions around Madison and to make comparisons as to the percentage of trees in each which show active exudation. These observations show that very few trees exhibit active bleeding in the lake region. Those along the lake shore show a very low percentage of bleeding. Those growing in wooded regions, as those back of University Hall and those out in wooded regions around Eagle Heights, show very little bleeding. However, those along the streets such as University Avenue, State Street, Carroll, Langdon, and Gilman Streets, as well as those along the sidewalks on

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the campus show a very high percentage of bleeding. They bleed in some cases to such an extent that the tree trunk is disfigured. The path of the liquid is marked by a line of white, bleached bark which may be due to precipitation from the sap or to the bleaching effect of some acid or alkali on the bark.

The question naturally arises as to why these trees along walks and streets show more bleeding than those along the lake or in natural woods. A possible reason would be that it is due to differences in the available soil water. If for instance, the trees along the walk or street have access to soil of lower water content than those under natural conditions, the osmotic concentration of the soil water would be increased. If there is constant leaching of the cement of the walk or street pavement, the concentration would be increased. The presence of artificial fertilizer might also produce this condition. In any case, if the amount of solution is increased, either by a relative decrease of water content or actual increase of solutes, the concentration of the soil water would be higher. This concentration of the soil water would in turn increase the osmotic strength of the root cells, for we know from the work of Renne (47) and Brosig (6) that a plant may adapt itself to growing in a more concentrated solution by increasing the concentration of its cell sap. If for example

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a plant which has become accustomed to growing in a one per cent KNO_3 solution is changed to a four per cent solution, it will soon adapt itself and take in water as usual. The concentration of the sap of the cells is raised to such an extent that it can overcome the added resistance from the outside. This rise of concentration in the cells will raise the pressure exerted on the individual cells and in case of injury due to freezing or mechanical injury the liability of exudation is very much increased.

Another possibility would be that of root injury. Kraus (33) and Wieler (62) find that if roots in potted plants are injured, bleeding may be induced. I have tried this experiment using potted plants of Pelargonium. Two pots were kept under separate bell jars for twenty four hours with the soil thoroughly saturated in order to obtain a maximum water content in the plants. At the end of this period the plants were cut off about an inch above the soil. The decapitated plants were left for a while to see if they bleed in the normal condition.

After finding the plants thus treated did not bleed, the roots were severed by means of a scalpel along one side of the plants, also wounding the main root. The other plants were left intact. The following day the injured root stalk showed active exudation, while the uninjured one remained dry on the cut surface. This bleeding continued during the day time for several days. I was, however, not able to

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duplicate these results with further trials. This bleeding, if it is due to root injury, might be explained by the fact that the corky layer of the roots is injured, which would permit the entrance of water into the root.more readily than in uninjured roots. In the case of the trees along the sidewalks or streets, there are many opportunities for root injury in reconstructing walks, laying sewers, and various building enterprises. The very growth of roots against these obstructions may injure them to some extent.

There is a possibility that the effect of gases in the soil may bring about exudation. Lepeschin (36) finds with his investigation on Pilobolus that such gases as chloroform and ether will, if administered in fairly strong doses, bring about bleeding. He also finds that ammonia will act in the same manner. There are many possibilities of poison being liberated from sewers and gas pipes along the streets and on the campus. One of the most common gases in our cities is coal gas, due to leaky gas mains. These gases might affect the membranes of the cells on the root hairs to the extent that they would bring about differences in the water content of the tree.

3. Geographical distribution of bleeding phenomena

During the early summer of 1917, I had an opportunity of observing the bleeding habit of elms at Iowa City, Iowa,

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while attending a summer session at Iowa University. It was evident that the percentage of elm trees which bleed was not nearly as high there as at Madison. Not nearly so many street trees showed bleeding and very few trees in the open. I noted several trees bleeding which were growing along a rocky hillside which would support the soil water concentration theory. The late summer of 1917 I spent in Kansas, and here again I was able to compare the distribution of bleeding in elms. I found that there was even a lower percentage here, showing bleeding than in Iowa. This naturally led me to conclude that the more severe freezing winters of the North may exert an injurious effect on the trunk.

I have not been able to get any data from the extreme South, but have corresponded with several men from Illinois, one from New York, and one from England. A. M. Augustine, secretary of the State Horticultural Society of Illinois writes that he has not noticed a great amount of bleeding of elm trees and states that he thinks it not as common there as farther north. E. P. Felt, State Entomologist of New York, writes that elm bleeding is quite common around Albany, New York. Reference to his observation will be made later. I received a letter from A. D. Webster of Regents Park, London, who has written several books on forestry and tree diseases. He writes that the elm bleeds quite frequently in England, due to some mechanical injury. Kraus (37)

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mentions it in connection with his experiments on twigs, but Wieler (62) does not include it in his list of bleeding plants. Most of the experimental work has been done on trees that show more active exudation.

4. Experimental data on young trees.

When I began work on this problem I ordered a half dozen young elms from a nursery, and had them set in candy buckets and put into the greenhouse. These trees were from four to six feet tall with a trunk about one inch in diameter at the base. They were planted in the greenhouse the second week in October, 1916. From that time continuing all winter I made slight wounds or cuttings on these trees to test for any exudation. In no case did the cut or wounded surface even become moist. This suggested that perhaps young trees or tissues do not bleed.

Assuming that perhaps there was a fungus growing in the forks of older trees which cause the wound, I collected some of this dead tissue by digging in with sterile instruments, and transferring the dead tissues to sterile dishes. Some of this material was plated out and some I attempted to inject into wounds made in the crotch of the young trees in the greenhouse. The plating showed the organisms to be only common air forms such as alternaria. The transplanting of

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the spores in the young trees had no visible effects as the wounds healed over in the months following and no bleeding took place.

5. Relation of root growth to bud formation.

Since the early spring activity of roots has been mentioned in connection with bleeding, I planted a tree in one of the pits in the greenhouses provided with a sloping glass base through which I could observe any root activity. The tree was planted December 1st. On December 15 white roots were visible along the glass plate. After the Christmas vacation I made regular observations and measurements on the growth of these roots. The roots were numbered and the growth lengths are shown in the following table:

Table of root growth

	Root 1	2	3	4	5	6	7
Jan. 11-13	1 cm.						
" 13-15	1 "						
" 15-17	.5"	2 cm.		1 cm.			
" 17-19	2 "	2 "	2 cm.	1 "	1 cm.		
" 19-22	1.5"	1.5	1.5	1.7	1.5	2.0 cm.	
" 22-24	.5		1	1	1	1	
" 24-26	.8				1	1.5	
" 26-29						2	
" 29-1						3	2 cm.
Feb. 1-3						2	1.7
" 3-5						1	1.4
" 5-7						1	1.8
" 7-12						3	1.5

The first signs of leaf formation were visible by the swelling of the buds of the tree planted in the pit on

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January 26. These results show two things: 1st, that the resting period of the tree had been shortened over two months; and 2nd, that root ~~formation~~ growth precedes bud growth by a month and a half. At no time before bud formation or afterwards was there any sign of bleeding.

6. Anatomy of crotches of young twigs.

Thinking there might be some anatomical peculiarity of the forks of elm I made various longitudinal and cross sections of young twigs. In many cases the vessels were coiled and doubled back, due to unequal growth, some appearing almost tied in a knot. I thought this might be due to the rupture in the forks. However, I made sections of box elder, ironwood, and various other trees which do not show this peculiar exudation from limb divisions and found vessels to be irregular and curved in the same way. Hence there was no object in following this line of investigation further.

7. Forced bleeding of sap wood.

Wieler was able to bring about bleeding in non bleeding plants by subjecting the plant to higher temperatures. For example, if a plant did not bleed at 20°C, it might be induced to bleed by immersing the soil and roots in water of 38° to 40°C. I made several trials with the trees growing in buckets to test out this possibility. By setting the buckets in a deep sink I was able to get the whole root

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system of the plant immersed in water at any desired temperature. After leaving the plant in water at 40°C for several hours, cuttings were made to test for any active exudation. In no case did the young cut tissues even become moist.

I have been able to get bleeding in the sense that Kraus (33) and Wieler (62) speak of bleeding. That is by immersing cut twigs of the elm in wet sand and keeping the whole covered with a bell jar, the surface of the twig showed a collection of small drops. However, in no case was there active running. I would not call this bleeding in the modern narrower sense of the term. In such cases the change of temperature under the bell jars may be sufficient to expand the gas content of the twigs and thus cause water to exude. I attempted twigs with young leaves attached but in no case did I get even a moist surface.

It would seem from these results that young elm trees do not possess the power of bleeding. My correspondence with observers in England, New York, and different parts of Illinois substantiates this. In no case, as far as I can learn, have nursery men observed bleeding from young trees.

8. The periodicity of bleeding of older trees.

The elms, unlike such common bleeding trees as maple,

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birch, and ironwood--does not show a definite period of bleeding in the spring. The two spring seasons (1917 and the present 1919), in which I have been able to make observations, have shown no active bleeding until early June, 1917, and May 23 for the present spring. On June 7, 1917, several trees were bleeding along the walk east from Main Hall. At the present time (May 26, 1919) several trees along University Avenue west of the campus show active exudation. Those bleeding from fresh cut large limbs showed the sap exuding from the middle of the limb from the heart wood. In no case did cuttings from small twigs show bleeding. As has been stated my observations were centered around Iowa City after June 12, 1917. On June 18, I noted several trees which showed active exudation in and about Iowa City. The bleeding was not regulated in any way by weather conditions. In many cases trees continued to bleed all night, but in all cases the bleeding was strongest in midday. I observed that the trees continued to bleed until the end of July, or the end of summer school, when I left Iowa for my home in Kansas. Here I observed active exudation through the month of August, and a part of September, although it was not as regular in early September as in August. During the autumn of 1916, I noted occasional bleeding. On October 19, 1916, about a third of

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the large trees on and about the campus at Madison were bleeding. Temperature observations preceding showed that October 17 and October 18 were cold, windy days. October 19 was a damp, warm spring like day. The change was quite sudden, hence in this case bleeding might have been due, to some extent at least, to expansion. Continued observation in October showed only a few trees bleeding, and these only slightly. In no case were young trees bleeding. There was no bleeding in the winter months of either season that I was able to observe.

These observations lead to two conclusions: 1st. That, contrary to the phenomenon of bleeding observed in almost all other plants, the elm does not bleed before leaves are formed in spring. 2nd. That it does bleed when the trees are in full foliage and that a reduction of transpiration is not necessary to bleeding as the trees bleed on the hottest and driest days of the summer.

9. Tissues concerned in bleeding

If the bleeding comes from young tissue or from the sap wood one should be able to produce active exudation by cutting off twigs or small limbs from older trees that show bleeding. During the two years that I have made observations I have made cuttings quite frequently. I also made holes in the outer tissue of the trunk by knife pricks, and never was able to get active exudation either during the period of active bleeding from the heart wood or during the non-bleed-

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ing period. During the spring months I have tested other trees such as the maple, box elder, ironwood, and birch. Slight wounds such as knife pricks into the pressure laden sap wood induced a gushing of sap from the sap wood, if the wounding was done during the specific bleeding period of the tree. It is a very common thing to see active running from woodpecker holes in the bark from other trees, but not, however, from the elm.

During the month of August, 1917, I conducted several experiments by boring holes in the trunks of trees on my father's farm in Kansas. I bored holes of various depths in several trees to test for exudation from sap and heart wood. All holes bored only to a depth of an inch or an inch and a half which pierced only the sap wood remained dry with no noticeable sap exudation. The wood in these wounds did not even become moist. Those wounds, however, which were bored to a depth of three or four inches, and which showed by the darkened colored wood that the heart wood was pierced showed active exudation. Into some of these holes, I inserted tight fitting sap spouts made by boring out a broom handle. The same results were obtained as before described. The spouts driven into the heart wood showed running, while those driven into the sap wood remained dry. Being many miles from any laboratory of any kind, I was unable to test this sap as to its composition. I repeated these wood tests by chopping into the trunk to

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various depths, and obtained similar results. If the axe penetrated the heart wood, sap exuded, but if only the white sap wood was wounded no running resulted.

Felt (17) describes a slender white maggot of the genia Mycetobia which can be found working in the bleeding crotches of elm trees. He describes them as being about one-fourth inch long with well developed jaws, with which they burrow into the tissue. The presence of dead organic matter favors the deposition of eggs and the development of small maggots which as they increase in size attack adjacent tissue which according to Felt soon produces bleeding.

To test out Felt's theory I bored holes by means of a brace and small bit into the forks of several trees to see if I could induce any bleeding. These trees have never shown any bleeding. The holes healed over and never even became moist. I found several kinds of larvae working in the wet tissues of trees at Iowa City. They, however, are there as a result of bleeding and not as a cause. I demonstrated this by boring into the forks of the trunk from which the sap was exuding. By boring into the trunk horizontally just below the fork I could observe, as the hole was being made deeper, from where the sap was coming. In each fork that showed bleeding there was a distinct layer of dead tissue showing the division of the two branches. By boring and chopping into various forks I was able to satisfy myself that there was no sap coming directly from the sap wood.

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I also cut down several trees and sawed sections at various angles through the fork. In every case I found either a pocket or this plate like strip of dead tissue at the forking of the branches. Just recently I noticed the sawed logs of a tree cut just north of the library on Langdon Street which, although it did not show any signs of previous bleeding showed a distinct break in the central woody tissue just below the fork.

Observations on sawed limbs both fresh and old, showed the sap to come from the center of the circle. By cutting into healed over wounds made by sawing limbs, I was able to locate a deep-seated pocket of dead tissue showing the source of the sap exuded.

10. Organic content of sap

The sap exuded is apparently almost pure water. While at Iowa I collected samples of the sap by absorbing with filter paper. (The flow was not excessive enough to collect in a vessel.) This I extracted by pressing and tested with Fehling's Solution. In no case did I get any reducing sugar, and in only one a slight test for non-reducing sugar. I ran controls with very dilute solutions of glucose to test the sensitiveness of the Fehling's Solution. It was found to be quite sensitive. I repeated the tests for sugar this spring and obtained like results. This corresponds to the researches

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of Sablon (50) who found very little sugar in extracted sap of the elm during the summer. The sap is colorless and tasteless. However, the very fact that the sap stains the tree shows that there must be some solute or solutes present. As has been pointed out the acid or alkaline content might have this effect. Very small amounts of solutes would be sufficient to bring about the stain as the sap runs for a long time, and the liquid is being continually evaporated thereby precipitating the small amount of solute on the bark which would bring about the coloration.

11. Discussion of significance and cause of bleeding

What then is the significance of the type of bleeding found in the elm for the tree? It is certain that the exudation pressure in this case and resulting sap movement cannot have any direct relation to bud formation, as many investigators have suggested, as bleeding only takes place after the leaves are formed. Nor can it be held that bleeding pressure charges the tree with its fullest capacity of water to guard against excessive transpiration during leaf formation, as there is no bleeding at this time. I have never been able to note any visible ill effects from bleeding to the elm tree. A. D. Webster writes from England that "trees that bleed profusely suffer greatly in health, though I have never been able to trace a death directly to that

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cause." There can be no doubt that the pathologic condition of the trunks noted must have a deleterious effect on the development of the tree.

Former investigators have shown that bleeding is accompanied by high pressures in the tree trunk. Early spring bleeding as shown by the maple is accompanied by high pressure, which apparently are the chief immediate causes of bleeding. However, it is generally conceded that, when the trees are in full foliage, and transpiration is rapid, there is a high negative tension in the trunk of the tree. I have found that the elm has this same negative tension in the sap wood. With the aid of Dr. Bennett I cut off under eosin solution various small limbs of elm to test for negative pressure. These experiments were performed during the heat of the day, while transpiration was rapid. By bending the limbs so that parts of them would be immersed in a shallow dish containing eosin solution, we were able to cut the twigs without getting any air into the vessels. After the limbs were severed, cuttings were made both away from and towards the tree trunk. It was found that the eosin was drawn by negative pressure a distance of several feet in the outer sap wood and eight inches in the inner in both directions from the cut. The fact that the dye traveled toward the tree almost the same distance as away from it excludes the possibility of the intake being due to immediate transpiration.

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There is a possibility that the elm has negative pressure only in the sap wood while in the heart wood there is either positive or at least, zero pressure. To test this I obtained permission to saw off a tree to test the relative pressures. A tree five inches in diameter at the base was selected. With the aid of Dr. Bennet a device was perfected for sawing the tree under a solution of dye. A wooden candy bucket was sawed in two and a hole made in the bottom of the size of the tree. The bucket was put together around the tree and drawn together tightly by twisting a rope around it. The bottom of the bucket was tightly sealed with plastecine, and the handle of the bucket roped to the tree in such a manner that there was room left to saw. The bucket was filled with dye and the trunk sawed by means of a common hand saw at such an angle that the entire cut surface of the trunk was immersed thereby excluding air from the vessels. The experiment was conducted in the early morning at sunrise, hence we would not expect as much negative pressure as was found with the small limbs.

Immediate cutting of the above treated trunk showed that the dye had penetrated the sap wood in both directions to a distance of about eight inches for the outer part and three to four inches for the inner part. The heart wood (which was only about an inch in diameter) showed no traces of the dye. These results show that there is negative pressure in the sap wood even in early morning when transpiration is at its minimum, but they also show that there is either positive

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or zero pressure in the heart wood. It is possible that this positive pressure in the heart wood can account for the exudation phenomena which I have observed.

If there is positive pressure in the heart wood one would expect a higher water content there also. I ran water content determination of this tree by using chips obtained by boring into the ends of the logs. Several samples were taken from the heart wood and several from each of three regions of the sap wood, viz., inner, near the heart of the tree, middle, and outer just inside the bark. The results showed the heart wood to contain 46% of moisture while the average for the sap wood from the three regions was 36%. The three regions of sap wood varied only one per cent, which might easily be due to experimental error. It is of interest here to note that the stump of this sawed tree is bleeding excessively both from heart and sap wood. I collected samples of this sap and tested for sugars. Only a trace of sucrose was found. The total amount of solutes, determined by evaporating the sap, was found to be only seven-tenths of one percent. This flow from the stump shows that if transpiration is entirely cut off at a time when the tree is in full foliage, the root pressure is sufficient to produce bleeding from the sap wood.

How then can we account for the observed negative pressure and low water content of the sap wood, and zero or

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positive pressure and high water content of the heart wood in actively transpiring trees? The heart wood of the tree may act as a water storage reservoir even while transpiration is active. This wood being composed of dead cells does not have the water retaining capacity of living cells, hence if the tissue is wounded in any way water runs out by slow filtration through the dead cells. It would seem that we have here a different phenomenon than that described by former investigations. Here we apparently have water drainage from a storage system which may continue for a long period of time and a phenomena that does not show a marked daily periodicity. In a final analysis, however, we are forced to consider the activities of living cells, otherwise, how can the continuous renewal of this storage water be accounted for? If there is negative pressure in the sap wood why does it give up any of its water to the heart wood and why doesn't the tree draw on the storage water in the heart wood during rapid transpiration? It has been shown in our historical reviews that Pfeffer gave three possible theories by which we might account for a continuous stream of water through a cell. The condition may be produced by: (1) differences in the permeability of plasma membrane on opposite sides of the cell, (2) differences in concentration of osmatic substance on the plasma membrane on opposite sides of the cell, (3) differences in the osmatic

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solution in the cell wall itself. It seems to me onewould have to appeal to one or a combination of these conditions to account for the flow of sap from the sap wood to the heart wood. If this flow is due to a difference of permeability between the inner and outer membranes of the sap wood cells one would expect the sap exuded to contain a fairly large amount of sugar. However, my results obtained from the sap of the bleeding stump shows that the sap of the tree at this season of the year has a very low sugar concentration in all regions of the wood. Growth is at a maximum at this time of year, hence all available food material is being utilized. There is very little solute present anywhere. Under these conditions, it might be possible for differences in the permeability of the membranes of sap wood cells to account for the inward flow of water. The second and third possibilities of Pfeffer's scheme seem to me less applicable because we would have to account for the continuous loss and replenishment of the osmotic substance in the membrane and wall. Wieler (62) believes that this continuous replacement of osmotic substances on the plasma membrane or in the cell wall is not only possible, but probable. I am inclined to believe with Lepeschin (36) that the permeability of the plasma membranes is the most plausible explanation.

It seems to me that one would have to explain the phenomenon of sap flow in the elm by some such appeal to the

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activities of living cells to supply the storage water in the heart wood. We cannot attribute bleeding to gas or wood expansion because it is a continuous exudation regardless of temperature fluctuations. High osmotic concentration in the wood cannot account for bleeding because we know that the sugar content is very low at this time of the year. Filtration phenomena may account for the outflow of sap from heart wood, because it is dead tissue, but they could not account for the continuous replenishment of the water to the heart wood. Babcock's (1) theory of the solubility of carbon dioxide in water at various temperature is not applicable because bleeding in this case is not dependent upon changes of temperature.

There are several possible explanations for the cause of the wounds in the heart wood. The first break in the wood may be due to growth cracks due to unequal growths in the forks, or to mechanical injury for example the swaying of the limbs by the wind. After decay begins bacterial action may set in and enlarge the pocket of dead tissue. I noted gas escaping from the fork of one tree which was actively bleeding. The gas bubbled up through the liquid just between the apex of the crotch. I increased the rate of gas escape by digging into the wound with a knife. This would seem to indicate that there was active fermentation in the pocket caused by some organism.

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Freezing might bring about the enlargement of a small growth pocket. If the heart wood has a fairly high water content we would expect some water to diffuse into these pockets. At low temperature this water would freeze and increase the size of the pocket by wounding adjacent cells. Hence there might be a combination of factors working to enlarge the pocket to such an extent that bleeding results.

Summer bleeding when trees are in full foliage is not limited to the elm. I have observed active exudation from oak (Quercus alba), maple (Acer saccharinum), and poplar (Populus balsamifera) during the month of June. In this case bleeding seemed to be coming from deep wounds also. Hence we would have to make a new classification of bleeding phenomena: 1st, trees which bleed from sap wood before leaf transpiration has begun, 2nd, trees which bleed from heart wood while leaf transpiration is active. The first type is influenced by meteorlogical change while the second type is not. Both types are dependent upon the action of living cells to produce active exudation.

IV. SUMMARY OF RESULTS

1. The elm tree bleeds from a definite wound either from a decayed limb or from the crotch fork of the trunk. The sap exuded runs down the tree trunk disfiguring the tree in many instances.

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2. The phenomenon of elm bleeding is more pronounced in the northern states than in the middle states, which suggests that freezing may be an important factor in wounding the tissues.

3. Elm trees growing along sidewalks and streets show a much higher percentage of trees that bleed than those growing in natural woods or along the lake front. This suggests the possibility of bleeding being caused by root injury or by concentration of soil water or its osmotic concentration.

4. Experiments to produce bleeding by wounding young trees in the green house gave negative results in every case. Young trees show no bleeding at any time.

5. Bleeding could not be induced in young trees by immersing the roots in water for several hours at a temperature of 40°C.

6. Observations of nurserymen and foresters of Illinois, New York and England substantiate the above statement that young trees do not bleed.

7. Elm trees show no daily periodicity. The trees were observed to bleed at twelve o'clock at night and early in the morning.

8. The yearly period of bleeding extends from the latter part of May to early October, with occasional bleeding in November.

9. Experimental data with cuttings, borings and choppings into portions of the trees connected with bleeding parts show

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the active exudation to come from the heart wood of the tree. Pockets of dead tissue were found in such bleeding portions.

10. Young branches cut off under eosin solution during the bleeding period show negative pressure.

11. A tree cut under eosin solution showed by the distances which the dye was sucked into the vessels, a negative pressure in the sap wood and a positive or at least zero pressure in the heart wood.

12. The water content of the heart wood of this cut tree was found to be ten percent higher than that of the sap wood.

13. The above results show a probability of the heart wood acting as a water storage reservoir during the summer months. The water content of the reservoir may be replenished by the action of the living cells of the sap wood.

14. The sap exuded in every case was found to be almost pure water, the total amount of solute not exceeding one percent.

15. There are two general types of trees which bleed. Those which bleed from sap wood in the spring before leaf formation, and those which bleed from the heart wood while leaf transpiration is active. The elm belongs to the latter class.

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